ADDITIONAL STUDIES OF *ASTER GEORGIANUS*, *A. PATENS*, AND *A. PHLOGIFOLIUS* (ASTERACEAE)

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ABSTRACT

Additional information is presented on the distributions, habitats, and associates of *Aster* section *Patentes*. Seven new counties are reported for *A. georgianus*, 28 for *A. patens*, and 16 for *A. phlogifolius*. *Aster georgianus* is described as a rare species of the southern United States, and deserving of additional studies to determine its federal status. *Aster patens* is a widespread species of the eastern United States and divisible into three geographic varieties. *Aster phlogifolius*, an Appalachian taxon, should be treated at the specific level because of consistent morphological, ecological, and physiological differences from *A. patens*.

RESUMEN

Se presenta información adicional sobre la distribución, habitats, y especies asociades de *Aster* sección *Patentes*. Siete nuevos condados son reportados para *A. georgianus*, 28 para *A. patens*, y 16 para *A. phlogofolius*. Se describe *Aster georgianus* como una especie rara de el sur de los Estados Unidos, la cual merece estudios adicionales para determinar su estado legal federal. *Aster patens* es una especie de amplia distribución de el oriente de los Estados Unidos y que se divide en tres variedades geográficas. *Aster phlogifolius*, un taxón de los montes Apalaches, debe ser tratado al nivel de especie debido a las diferencias consistentes de morfología, ecología y fisiología sobre *A. patens*.

INTRODUCTION

Three species were recognized in *Aster* section *Patentes*: *A. georgianus* Alex., *Aster patens* Ait. (with three varieties), and *A. phlogifolius* Muhl. ex Willd. (Jones 1983). Most previous workers had considered all these taxa as conspecific with *A. patens*. Because *A. georgianus* is now known to be a decaploid species (2n=50) with a distinct morphology, it has been generally accepted as a distinct species associated with the Piedmont of North and South Carolina, Georgia, and Alabama. The Georgia aster has been receiving increased attention since being listed as a Category 2 taxon on the Federal Register (USFWS 1990), and I have received a number of requests in the last two years for more information on the taxon. Species status for *A. phlogifolius*, however, has met with less acceptance, especially from some of the major workers in the genus (A. Jones and Hiepko 1981 and A. Jones pers. comm.; Semple 1984; Gleason and Cronquist 1991). *A. phlogifolius* and *A. patens* are identical in chromosome number (2n=20) in the areas of range overlap, and they can cross. In my opinion, they do exhibit distinct morphological, physiological, and ecological characters. The objective of this paper is to update the available information on all the taxa in *Aster* section *Patentes* and to provide additional data to support the existence of genetic and taxonomic differences between *A. phlogifolius* and *A. patens*.

MATERIALS AND METHODS

Additional information on distributions and associates of these taxa was accumulated through field studies and herbarium searches. Vouchers from field work have been deposited at EKY. The following herbaria were consulted to provide additional distributional information: BEREA, EKY, FLAS, WIS, UNA, US and VDB (Holmgren et al 1990).

Achenes representative of each taxon were photographed at 100X using a Scanning Electron Microscope at Auburn University. For seedling comparisons, achenes were planted in sand and allowed to germinate, removed at the emerging radicle stage, the cotyledon stage, and the 3rd cauline leaf stage, and drawings were made of each stage.

Germination studies were conducted on achenes collected from contiguous populations of *Aster patens* and *A. phlogifolius* in Rowan County, Kentucky, and from another population of *A. patens* in Menifee County, Kentucky. The basic procedures of Baskin and Baskin (1979) were followed, using at least 50 achenes per petri dish, two or three replications per treatment, and monitored for 16 weeks.

RESULTS AND DISCUSSION

Aster georgianus: Distribution and Associates

A total of 21 counties have been mapped for *Aster georgianus*, but it was noted that extant populations were known from only nine sites (Jones 1983). Further field and herbarium studies since 1983 have resulted in the documentation of the following new counties: **Alabama**. Shelby County, *Kral 68027* (VDB). **North Carolina**. Gaston Co., 7 Oct 1902, *collector unknown*, (US) Rowan Co.: *Jones 4602* (EKY). **South Carolina**. Lauren Co.: *Jones 4631* (EKY); Union Co.: *Jones 4622* (EKY); and York Co.: *Jones 4620* (EKY). Semple (1984) reported the species with its decaploid count of 2n=50 from Oconee Co., South Carolina. Alan Weakley, North Carolina Natural Heritage Botanist, reports finding this plant in Mecklenberg County, North Carolina (pers. comm.). Thus *A. georgianus* has been reported from 29 counties, but only 16 extant populations have been located during the last 15 years.

Isotypes of *Aster georgianus* were not listed in my 1983 paper, but a duplicate of the 1898 Cuthbert collection from Richmond Co., Georgia, has subsequently been located at FLAS.

Most of the known populations of *Aster georgianus* are small, consisting of colonial stands of 10 to 100 stems. It is likely that these stems represent just a few genotypes at each site. The populations occur along dry, fairly open roadsides in communities dominated by *Quercus falcata* Michx., *Q. alba* L., *Q. coccinea* Moenchh., *Q. stellata* Wang., *Liquidambar styraciflua* L., *Nyssa sylvatica* Marsh., *Prunus serotina* Ehrh., *Pinus echinata* Mill., *P. taeda* L., *P. virginiana* Mill., *Cornus florida* L., and *Sassafras albidum* (Nutt.) Nees. Herbaceous species at these sites included *Aster patens* Ait., *A. grandiflorus* L., *A. undulatus* L., *Arnica acaulis* (Walt.) BSP, *Chrysopsis graminifolia* (Michx.) Elliott, *C. mariana* (L.) Elliott, *Helianthus angustifolius* L., *Solidago erecta* Pursh, *S. nemoralis* Ait., *Agalinus purpurea* (L.) Pennell, *Scutellaria alabamensis* Alex., *S. elliptica* Muhl., *Lobelia puberula* Michx., and *Erianthus contortus* Baldw. Alan Weakley (pers. comm.) views *Aster georgianus* as a relict species of post oak-savanna communities that were once fire-maintained in North Carolina. He has found other federally listed plants in association with *A. georgianus*, including *Helianthus schweintzii* Torrey & Gray, and *Lotus purshianus* (Bentham) Clements & Clements var. *helleri* (Britt.) Isely, both Category 2 taxa on the Federal Register (USFWS 1990). Weakley also reports that most of the known sites for *A. georgianus* in North Carolina harbor only a few plants, and some have recently been influenced by habitat disturbance.

Aster patens: Distribution and Associates

Aster patens is a widespread species of the eastern U.S. It can be divided into three fairly well-marked varieties: var. *patens*, the common tetraploid (2n = 20) east of the Mississippi River; var. *patentissimus* (Lindl.) Torrey & Gray, the common tetraploid of the Ozarks and adjacent areas; and var. *gracilis* Hooker, the primarily diploid (2n = 10) taxon of the southwestern portions of the range. Further chromosome counts of these taxa by Semple (1984) supported my postulate that diploid plants occur only as far east as central Alabama.

Field and herbarium studies have resulted in the following county records for the var. *patens* that were not mapped in Jones (1983):

Arkansas. Miller Co.: *Palmer 14621* (US). **Kentucky.** Barren Co.: *Johnson 1047* (EKY); Elliott Co.: *Jones 4590* (EKY); Estill Co.: 10 Oct 1978, *Martin* (EKY); Harlan Co.: *Thompson 87-1724* (BEREA); Hart Co.: *Braun 3606* (US); Lawrence Co. *Jones 4575* (EKY); Lee Co.: *Thompson 85-1639* (BEREA); Letcher Co.: *Braun 827* (US); Madison Co.: *Braun 597* (US); Menifee Co.: *Jones 4385* (EKY); Rockcastle Co.: *Godbey 585* (EKY); Whitley Co.: *Braun 2621* (US). **Maryland.** Allegheny Co.: 20 Sep 1881, *Smith* (US). **Ohio.** Adams Co.: 6 Oct 1965, *Braun* (US). **Oklahoma.** Logan Co.: Aug 1891, *Carlton* (WISC). **North Carolina.** Craven Co.: *Kearney 2208* (US). **New York.** Dutchess Co.: Sep 1875, *Scribner* (US). **South Carolina.** Anderson Co.: *Davis 8497* (US). **Virginia.** Bath Co.: 9 Sep 1907, *Steele* (US); Rockbridge Co.: 11 Sep 1904, *Steele* (US).

New documentation for county records of var. *gracilis* is as follows:

Alabama. Autauga Co.: *Gunn 1202* (UNA); Lowndes Co.: *Gunn 1371* (UNA); Wilcox Co.: *Gunn 1344* (UNA). **Kansas.** Gray Co.: *Carlton 429* (US). **Mississippi.** Attala Co.: *McDougall*

1147 (US); Madison Co.: *McDougall 1487* (US). **Oklahoma**. Choctaw Co.: 13-15 Oct 1896, *Schuchert* (US). The Gray County, Kansas record for the var. *gracilis* represents the furthest known westward extension of the species. No new counties were found for *Aster patens* var. *patentissimus*.

Aster patens is found in a variety of habitats (Jones 1983). In its southern range it can be found with many of the same associated species as listed above for *Aster georgianus*. The species is primarily one of woodland edges and disturbed areas, often occurring in partial to full sun.

Aster phlogifolius: Distribution and Associates

Aster phlogifolius is a tetraploid species closely associated with Appalachian habitats. It was mapped from southern New York across Pennsylvania to northern Ohio to southern Indiana to northeastern Alabama (Jones 1983). The following counties represent additions to the known distribution:

Kentucky. Bell Co.: *Thompson 85-1672* (BEREA); Estill Co.: *Guetig 382* (EKY); Jackson Co.: *Abner 91-2* (EKY); Laurel Co.: *Thompson 88-2819* (BEREA); Lee Co.: *Thompson 85-1638* (BEREA); Lewis Co.: *Braun 4387* (US); Rowan Co.: *Braun 1671* (US). **Maryland**. Garrett Co.: 4 Oct 1878, *Smith* (US); Kensington Co.: *Standley 5951* (US). **Ohio**. Montgomery Co.: *VanCleve* (US). **Virginia**. Allegheny Co.: *Leonard 16986* (US); Augusta Co.: *Steele 161* (US); Nelson Co.: *Steele 44* (US); Page Co.: *Walker 2682* (US). **West Virginia**. Pendleton Co.: *Killip 36060* (US).

Aster phlogifolius is typically found in more mesic habitats than *A. patens*, often above cool streams on shaded, boulder slopes. Typical associates include *Quercus alba* L., *Q. rubra* L., *Tsuga canadensis* (L.) Carr., *Acer rubrum* L., *A. saccharum* Marsh., *Fagus grandifolia* Ehrh., *Magnolia acuminata* (L.) L., *M. tripetala* L., *Aster shortii* Lindl., *Polymnia canadensis* L., and *Polygonatum biflorum* (Walt.) Ell. Population contact between *Aster phlogifolius* and *A. patens* may occur in the event of habitat disturbance, i.e., power-line cuts or road building and there are usually a few individuals that appear to be hybrids. Nevertheless, there is no evidence of a high degree of introgression, and in every case the taxa can still be easily distinguished by characteristic morphological features (Jones 1983). At one such site in Rowan County, KY (the one sampled for achene germinations, see below), the populations of *Aster phlogifolius* and *A. patens* occurred along a south-facing slope over about a two km stretch of gravel road. The former species was mostly restricted to the more shady, protected areas of the upper slopes, while the latter occurred along the right of way, often in full sun. In some cases individuals of each taxon occurred side by side.

I have spent a considerable amount of time searching for large populations of *A. phlogifolius* in eastern Kentucky, but with very little success. Some sites where it once occurred in Tennessee have now been destroyed, and at others the populations are barely persisting. This species is very intolerant of habitat disturbance, and as the percentage of relatively undisturbed Appalachian forest declines, so will the abundance of this plant.

Achene and Seedling Morphology

While the achenes of *Aster patens* and *A. georgianus* differ only in size, those of *A. phlogifolius* are distinctly different (Jones 1983). Scanning electron photographs of the lower portions of the achenes are included here to present further evidence of these differences (Fig. 1). Achene trichomes of *A. phlogifolius* are much more restricted to the achene ridges, thus appearing to be in rows, and are more appressed and shorter (less than 0.4 mm long) than those of *A. georgianus* and *A. patens*. *A. phlogifolius* achenes also are bulkier and darker, varying to black. These consistent mature achene features are important taxonomic characters for *A. phlogifolius*, and are probably often overlooked by those attempting to separate this taxon from *A. patens*.

A brief mention of seedling leaf differences between *A. patens* and *A. phlogifolius*, and a photograph of young rosette leaves were presented in Jones (1983). A series of line drawings are given to emphasize the fact that these differences are exhibited from the time the first cauline leaf emerges above the cotyledons (Fig. 2). *A. georgianus* seedlings are larger than those of *A. patens*, but are otherwise very similar. The seedlings of these asters possess a short hypocotyl which raises the cotyledons slightly above the ground. The cotyledons are ovate-spathulate to orbicular-spathulate, and the first few seedling leaves in both are lanceolate-attenuate, and pubescent. The young cauline leaves of *A. phlogifolius*, when compared with those of *A. patens*, are thinner, with more pronounced veins, and with longer, curlier trichomes, thus foreshadowing the later characteristic leaf features of the species.

Achene Germination

An earlier study lead to the conclusion that the achenes of *A. patens* and *A. georgianus* germinated very easily but that the those of *A. phlogifolius* required a cold treatment for good germination (Jones 1983). After a reexamination of the data and another series of experiments, these conclusions now must be modified. A two-week germination study in 1979, using two populations of each taxon as achene sources, with standard techniques, at 14 hour photoperiods, found the following:

1) In *A. patens* 56, 87, and 76% achene germination was achieved at 15.6/4.4, 21/10, and 26.6/15.6° C, respectively, without stratification.
2) In *A. phlogifolius* 10, 28, and 61% achene germination was achieved at the above temperatures, without stratification.
3) The achenes of both taxa germinate maximally (over 90%) at 15.6/4.4 and 21/10° C after being subjected to a 12-week stratification period at 4° C.

In 1985, further studies on the achene germination of *A. patens* and *A. phlogifolius* were carried out at the laboratory of Jerry and Carol Baskin at the

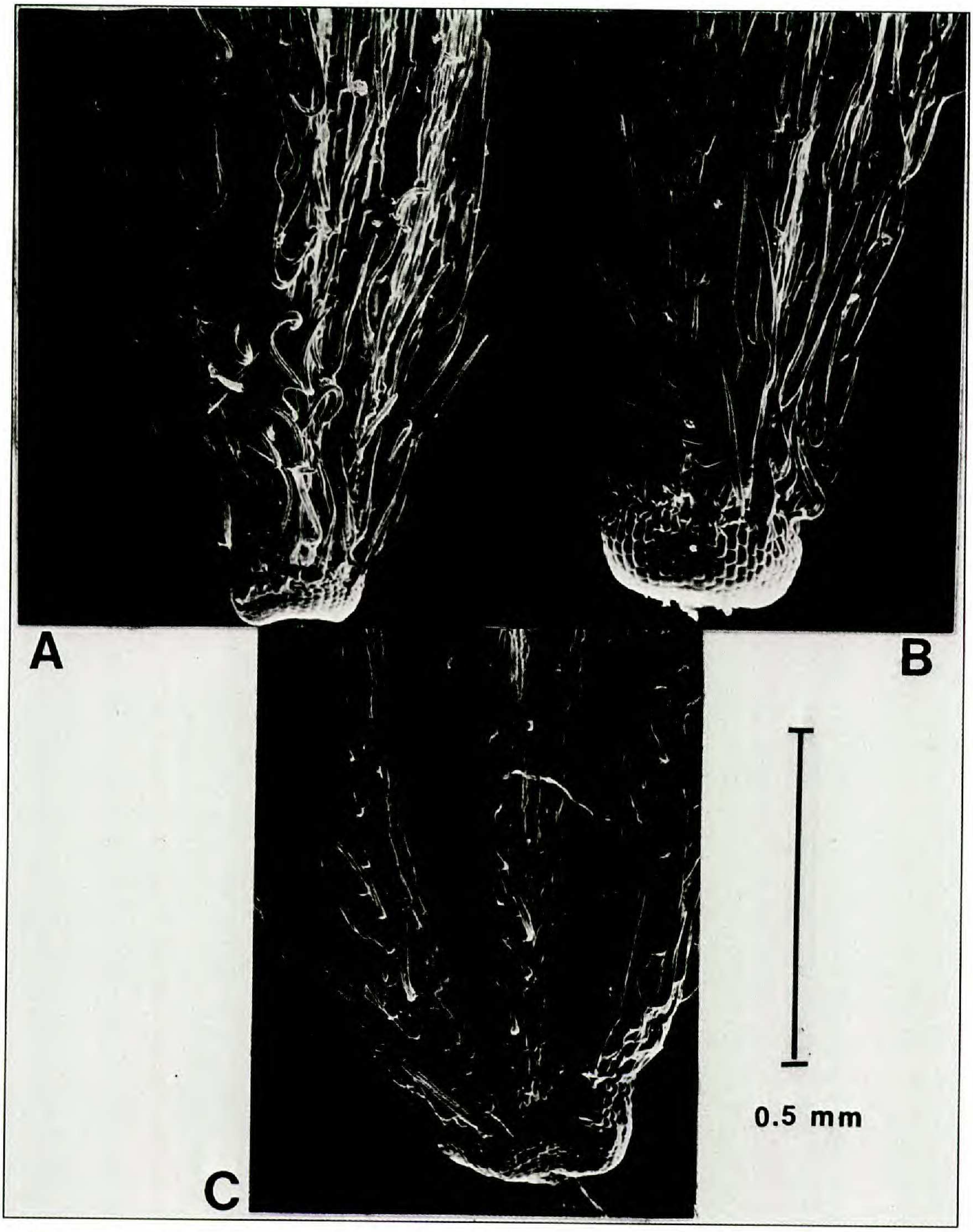

FIG. 1. Scanning electron photographs (100X) of achene bases of *Aster patens* (A), *Aster georgianus* (B), and *Aster phlogifolius* (C).

University of Kentucky. The results are presented in Table 1. These data show a comparison between adjoining populations of *A. phlogifolius* and *A. patens* in Rowan County, Kentucky, and another population of *A. patens* from Menifee County, Kentucky. The following is a summary of the results:

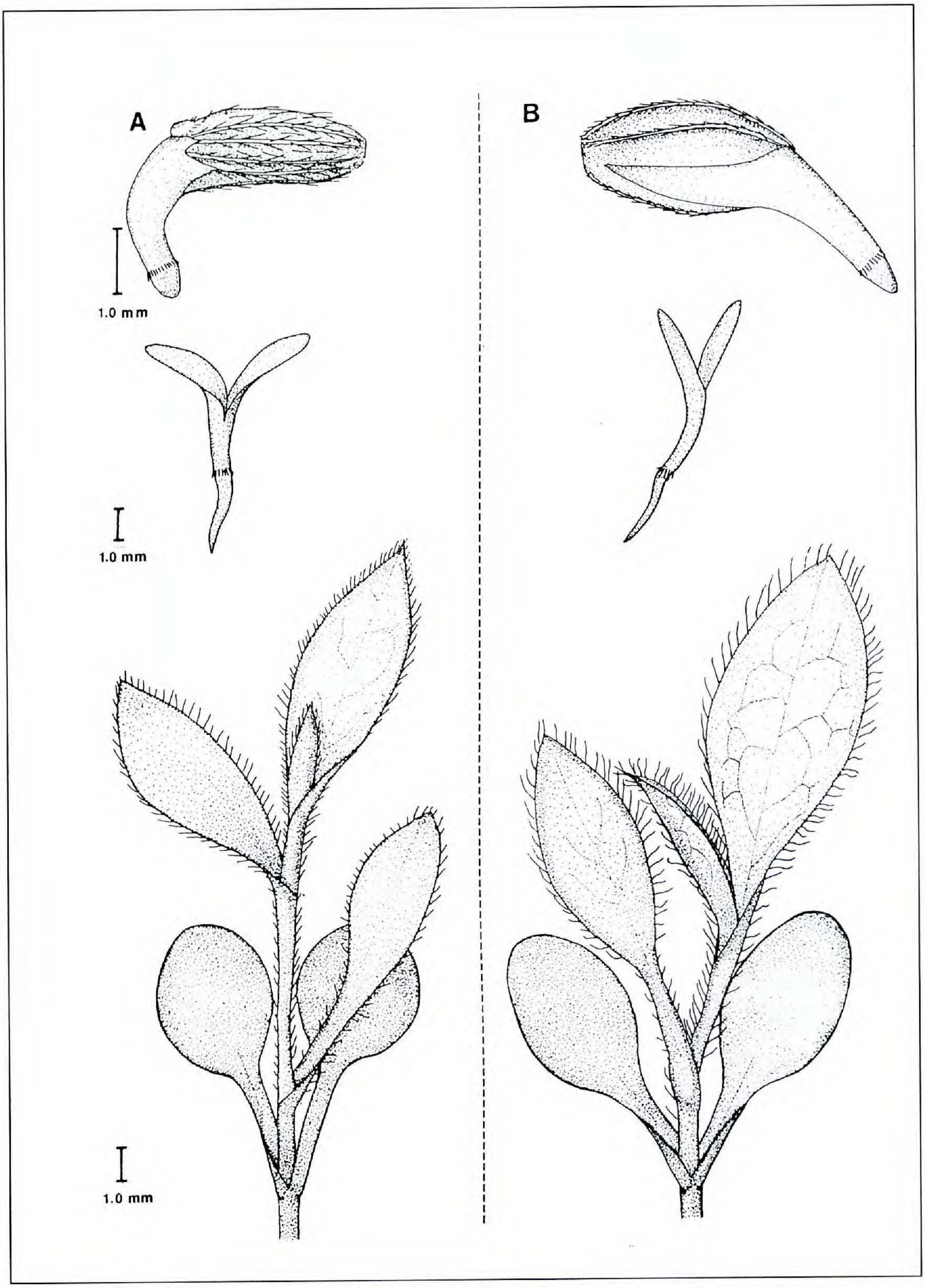

FIG. 2. Young seedling development in *Aster patens* (A) and *Aster phlogifolius* (B).

1) Both populations of *A. patens* had almost identical patterns of germination, with near-maximal germination after two weeks at all regimes from 15/6 to 30/15° C, but showing some decrease at 35/20° C.

TABLE 1. Achene germination percentages (mean + SD) of *Aster phlogifolius* and *A. patens*. Techniques of Baskin and Baskin (1979) were used except that the middle column of data is based on a duplicate set of dishes instead of a triplicate set.

Temp (c) and Weeks (W)	*A. phlogifolius* Rowan County	*A. patens* Rowan County	*A. patens* Menifee County
15/6			
2W	2 ± 3	75 ± 2	93 ± 5
8W	21 ± 10	95 ± 7	96 ± 2
16W	84 ± 9	97 ± 4	96 ± 2
20/10			
2W	5 ± 4	100	100
8W	25 ± 10	—	—
16W	25 ± 13	—	—
25/15			
2W	12 ± 4	96 ± 3	90 ± 4
8W	15 ± 5	100	98 ± 1
16W	17 ± 6	—	98 ± 1
30/15			
2W	65 ± 26	96 ± 6	98 ± 1
8W	78 ± 20	100	100
16W	78 ± 20	—	100
35/20			
2W	43 ± 30	55 + 1	83 ± 15
8W	46 ± 30	62 ± 6	83 ± 15
16W	49 ± 30	63 ± 4	83 ±15
Pretreatment 5 C for 12W			
15/6			
2W	35 ± 12	100	100
4W	100	—	—
20/10			
2W	100	—	—
4W	100	—	—
25/15			
2W	98 ± 2	—	—
4W	100	—	—
30/15			
2W	99 ± 1	—	—
4W	100	—	—
35/20			
2W	59 ± 35	—	—
4W	60 ± 35	—	—

2) *A. phlogifolius* showed a very different pattern, with rates of under 25% at 15/6 (except at 16 weeks), 20/10, and 25/15° C, rates of 65-78% at 30/15° C, and 42-49% at 35/20° C. In the 15/6° C treatment, the germination totals nearly doubled between 10 and 16 weeks, up to 84%. It appears, therefore, that this 15/6° C treatment actually stratified the achenes, and stimulated germination after a period of 10 – 12 weeks. As in *A. patens*, germination was stimulated by moderate warmth (30/15° C) but inhibited by greater heat (35/20° C).
3) Both taxa showed generally maximal germination either during or after a cold treatment of 12 weeks. All of the achenes of *A. patens* germinated during the cold treatment. About 30% of *A. phlogifolius* achenes germinated during the cold treatment, the remainder soon thereafter at all regimes except the hottest.

Thus the results obtained in experiments conducted in 1979 and 1985 are very similar, but a more accurate conclusion based on both sets of data can now be stated: the freshly matured achenes of *A. patens* are nondormant, while those of *A. phlogifolius* are conditionally dormant and thus germinate to 50% or more only above 30/15° C. Therefore, *A. phlogifolius* achenes require a cold treatment for good germination *at low temperatures*, but not at warmer temperatures. Stratification lowers the minimum temperature for germination of *A. phlogifolius* achenes, and this effect was noted by Baskin and Baskin (1988) for nearly all tested Compositae achenes with low-temperature dormancy at maturity.

The germination patterns of these two species may be correlated with their distributions. *A. phlogifolius* is primarily an Appalachian taxon, and these populations have become adapted to an alternating cold/warm season climate. The low temperature dormancy would prevent large numbers of achenes from germinating in the late fall, with subsequent seedling loss over the winter. The achenes would experience natural stratification over the winter, and would then be able to germinate during the cool temperatures of the early spring, allowing enough time for seedling establishment prior to summer drought. Baskin and Baskin (1988) found a similar strategy existed among many herbaceous plants of mesic forests.

Aster patens is primarily a southern species that occurs in a variety of upland and lowland habitats. It is much hardier, more weedy species than *A. phlogifolius*. With nondormant achenes it is likely that seedling establishment does take place in the fall, especially in the more southerly parts of its range. Whether fall-germinated seedlings can survive the colder winters in the northerly habitats of the species is not known. These achene germination patterns may be indicative of a more specialized adaptive system in *A. phlogifolius* and a more generalized adaptive system in *A. patens*. Achene germination differences do exist, and further point toward the genetic and physiological divergence of these two taxa.

CONCLUSIONS

Aster georgianus has been collected from only 16 counties in the southeastern U.S. during the last 15 years. It is likely to have originally inhabited oak-savanna type communities, but with the disappearance of these habitats, it now persists primarily along open or partially open savanna remnants, woodland borders and roadsides. The species is unique among base-5 asters, being the only known decaploid, and its phylogenetic relationships with *A. patens* and other similar asters are unknown (Jones 1983; Semple 1984). More detailed studies are needed on habitat requirements, demography, genetics, and distributions. Currently a Category 2 plant on the Federal Register, *A. georgianus* deserves a high priority as the subject of a status survey report by the United States Fish and Wildlife Service.

Aster phlogifolius is obviously very closely related to *A. patens*, and the question arises as to subspecific or specific treatment. Leaf, phyllary, floret, and achene differences provide consistent taxonomic markers. Leaf differences are evident from the very early stages of seedling growth. Further evidence of genetic divergence is suggested by the differences in habitat, reactions to disturbance, and in achene germination. They have not diverged sufficiently to prevent crossing, but these tetraploid Appalachian populations have developed their own evolutionary lineage and have accumulated sufficient genetic differences through ecological isolation to make them morphologically different. Therefore, I still maintain their treatment as different species. Species status would draw more attention to this taxon, which could be used as an indicator species of mesic Appalachian communities. Recent field studies suggest that this plant is on the decline in many areas, and its loss should be of concern to those interested in preserving the rich assemblage of species that occur in our Appalachian forests.

Aster patens and related taxa provide a good model for studying the evolutionary processes of polyploidy, hybridization, and ecological/geographic isolation that have occurred in the base-5 asters. From southwestern diploid ancestors have arisen wide-ranging tetraploids with subsequent divergence in the Appalachian and Ozarkian regions, and the production of a high polyploid with a unresolved ancestry. Additional studies are planned in order to develop a better understanding of the biology and relationships of the taxa in *Aster* section *Patentes*.

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